

GROWTH AND FUNCTION OF SPINES IN THE JURASSIC AMMONITE *ASPIDOCERAS*

by A. CHECA and D. MARTIN-RAMOS

ABSTRACT. The structure, mode of growth, and possible function of the spiniform tubercles of the Upper Jurassic ammonite *Aspidoceras* are described and analysed. Their complex growth pattern is particularly suitable for the construction of long, delicate, hollow spines. These spines probably contained extensions of the mantle, which were in contact with the environment through openings at their tips. Their function is thus inferred to have been primarily sensory.

THE wide diversity in ornamentation to be found in ammonites implies that the adaptive strategies, although recurrent, were very varied. Among the many hypotheses put forward, even the most consistent are but general models which, when applied to specific cases, have to be modified.

Ammonites have three basic forms of macro-ornamentation: ribs, tubercles and keels. The tubercles vary greatly both in shape and size throughout the Mesozoic, from short, bulky, extraordinarily reinforced ones to hair-like spines, and it is to be presumed that this wide morphological and structural range reflects different functions.

In this work we study the structure and mode of growth of the spiniform tubercles of the Upper Jurassic ammonite genus *Aspidoceras* and offer some suggestions as to what their function may have been.

INTRODUCTORY REMARKS

A brief description of the genus Aspidoceras.

The genus *Aspidoceras* (Zittel), belonging to the superfamily Perisphinctaceae (Steinmann), includes both evolute and semi-involute forms, ranging from the minute to the gigantic in size. The whorl cross-section may be either equidimensional or depressed and varies in shape from subquadrate to oval or reniform. The body-chamber usually occupies half a whorl or a little more.

The ornamentation of this genus consists of two rows of spines, one periumbilical and the other mid-flank or lateroventral (text-fig. 1A). Within the genus there are two clearly distinguishable morphotypes: one with two rows of spines throughout ontogeny and another with lateral ornamentation that disappears in the outer whorls.

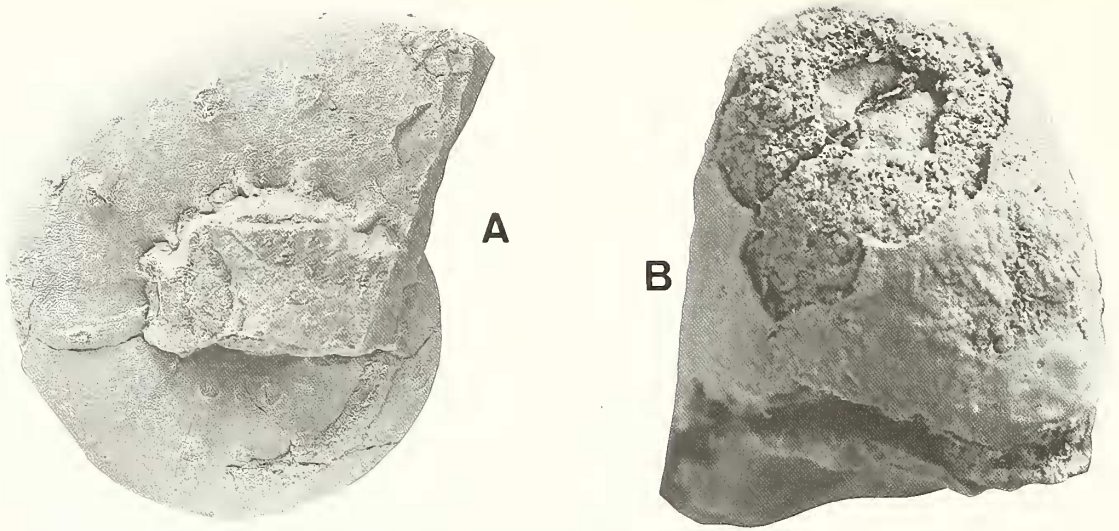
This study involves the more frequent species of the genus, all of them belonging to the morphotype that maintains two rows of tubercles throughout the entire ontogeny.

Aspidoceras extends from the Bimammatum Zone of the Upper Oxfordian to the Jacobi Zone of the Lower Berriasian, and in some levels of the Lower to Middle Kimmeridgian its geographical dispersion is worldwide.

MATERIAL AND TECHNIQUES

The material studied was taken from five Kimmeridgian outcrops of condensed biomicrites in the Subbetic Zone (Betic Cordillera, SE Spain) which have been assigned the following labels: AC₂₁ (Alta Coloma, province of Granada), UB₁ (Ubrique, province of Cádiz), AM₁, AM₂ (La Almola, province of Málaga) and CS₁ (Castillones, province of Málaga). Their precise location is given in Checa (1985, p. 29).

The specimens are very well preserved and the calcite shells retain vestiges of quite delicate



TEXT-FIG. 1. A, *Aspidoceras longispinum* (Sowerby), U.AM₁.R.23, lateral view, La Almola (province of Málaga), Middle–Upper Kimmeridgian, $\times 1$. B, *Aspidoceras hystricosum* (Quenstedt), U.UB₁.2.46, isolated external tubercle showing distal aperture (umbilical view), Ubrique (province of Cádiz), Upper Kimmeridgian, $\times 7.5$. Specimens coated with ammonium chloride.

structures, although, because of the compactness of the biomicrite, the spines are not often easy to extricate and thus many of the samples have had to be studied in sections.

In all, 84 specimens of *Aspidoceras* have been studied, together with 14 individuals of the genus *Orthaspidoceras* (cf. Checa's systematic revision, 1985), which came from the same outcrops and levels, for comparative purposes. All of them are deposited at the Department of Stratigraphy and Palaeontology of the University of Granada.

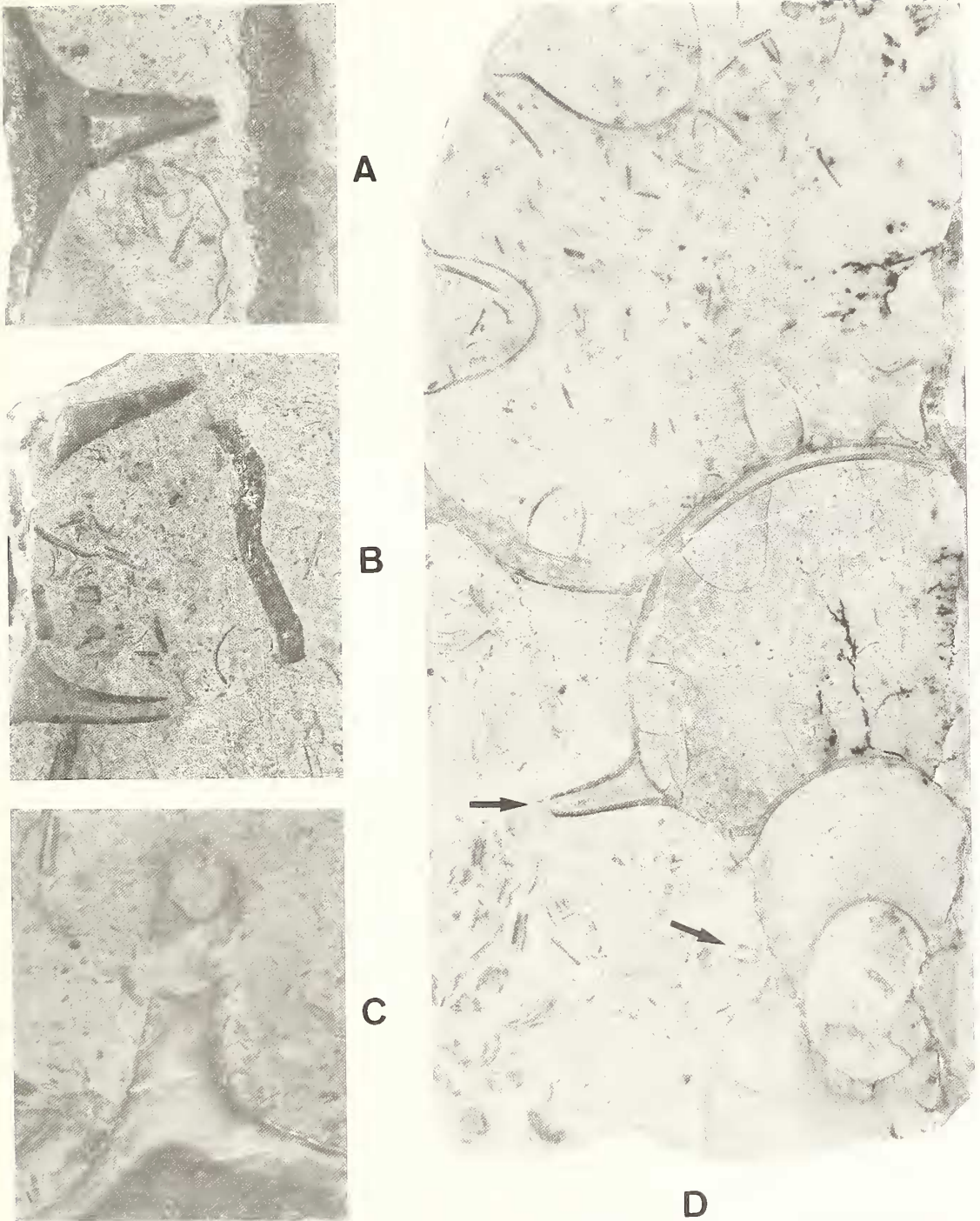
High-resolution techniques have been used for this study. The mineral composition of the shell was determined by X-ray diffraction, using a Philips PW 1710 automatic powder diffractometer. The {110} pole figure of the calcite was obtained by means of an automatic texture attachment (Philips PW 1078/24). Intensity corrections for X-ray pole figures have been made. The mineralogical analysis also involved observation by transmission electron microscopy (TEM), using a Zeiss EM10C. Lastly, the distribution of the growth lines and the external morphology of the isolated tubercles were examined by scanning electron microscopy (SEM, Zeiss DSM 950).

DESCRIPTION AND GROWTH PATTERN OF THE TUBERCLES

Description

The spiniform tubercles of *Aspidoceras* are slightly conical in shape and project either perpendicularly or rursiradially from the whorl. Sometimes they start off at an angle and bend outwards until they end up growing perpendicularly to the equatorial plane of the spiral (text-figs. 1A and 2B, D). They vary in length as the shell grows, being comparatively longer and thinner in the more juvenile stages than in the mature ones.

The spines are arranged in two separate rows, one of them umbilical and the other either mediolateral or ventrolateral, and normally there are more spines in the outer row than the inner one. Thus the longitudinal distance between each of the tubercles in the umbilical row is the same as that between those of the ventrolateral one. Wherever the spines in either row are synchronous they are usually joined by a weak rib. The number of tubercles per whorl is a very variable intraspecific parameter.



TEXT-FIG. 2. A, B, *Aspidoceras sesquinosum* Fontannes, U. AM₁.1.4, La Almola (province of Málaga), Lower Kimmeridgian; longitudinal sections of a lateral (A, $\times 3.2$) and an umbilical tubercle (B, $\times 3.5$). C, *Aspidoceras hystricosum* (Quenstedt), U. AC₂₁.51.77, longitudinal section of a lateral tubercle, Alta Coloma (province of Granada), Middle-Upper Kimmeridgian, $\times 3.6$. D, *Aspidoceras binodum* (Oppel), U. AM₁.B.23, section showing two umbilical tubercles with distal aperture (arrows), La Almola (province of Málaga), Lower Kimmeridgian, $\times 4.1$.

The wall of the tubercle itself is composed of the outer prismatic and the nacreous layers of the shell. The inner prismatic layer forms the basal septum, or floor, which closes the bottom of all the tubercles up to about half the length of the body-chamber from the aperture (text-fig. 5), as has been described in several tuberculate ammonites (e.g. Kennedy and Cobban 1976, p. 28; Birkelund 1981, p. 194). The latter author stated (1981, p. 190) that the closure of the tubercles of immature specimens does not go as far along the body-chamber, but our evidence is inconclusive on this point. The basal septum gives the tubercles their characteristic mammiform appearance when only the internal mould survives.

The most striking feature of the spines is that not only are they hollow but they are also open at their distal tips. This is clearly evident from a study of more than twenty sections made along the axes of spines still encased in the rock (text-fig. 2) and can in no way be attributed to the rough handling of the samples or to careless dissection from the matrix. Some larger spines, which it has been possible to free undamaged from the matrix, have circular or slightly elliptical openings at their points (text-fig. 1B; Pl. 76, figs. 3 and 4). These holes may of course be due to taphonomic or diagenetic processes resulting in the loss of shell-covering at the point of the spines, and indeed a minute examination of some specimens does reveal that the borders are sharp and irregular, indicating breaking or diagenetic dissolution (occasionally they are found associated with stylolitic surfaces). Nevertheless, in many other cases the edges are smooth and rounded and sometimes converge gradually towards the axis of the spine, indicating that no later external process has altered their original morphology. Added to this, we have never come across a single clearly closed specimen in all our material. Thus we believe it reasonable to conclude that the spiny tubercles of *Aspidoceras* had an opening at their tips in life.

Mineralogical composition and texture

The mineralogical composition has been determined by X-ray analysis of a tubercle removed from the shell and also a fragment of shell wall of a specimen of *A. longispinum* (Sowerby) (U.AC₂₁.5b.37). Care was taken not to include any of the matrix and the sample was ground only lightly so as to avoid making any polymorphic transformations. The diffractograms show that in both samples all the original carbonate has been completely transformed into calcite.

An X-ray diffraction textural analysis performed on an umbilical spine of *A. sesquinosum* Fontannes (U.AM₁.1.4) revealed the preferential orientation of the existing calcite crystals, which indubitably reflects the orientation of the original carbonate crystals (text-fig. 3). This remnant orientation has also been confirmed by the constancy in the orientation of the reciprocal lattice as observed directly by TEM at various points within the outermost material (possibly the outer prismatic layer) of a spine of *A. longispinum* (Sowerby) (U.AM₂.5.40). The crystallographic *c* axis is always parallel to the generatrix of the spine.

If we assume that the orientation of the *c* axis, perpendicular to the (CO₃)⁻², has remained stable throughout the transformation of the aragonite or vaterite into calcite, which is almost certainly the case, the original crystals were aligned parallel to the wall of the tubercle. This orientation is clearly

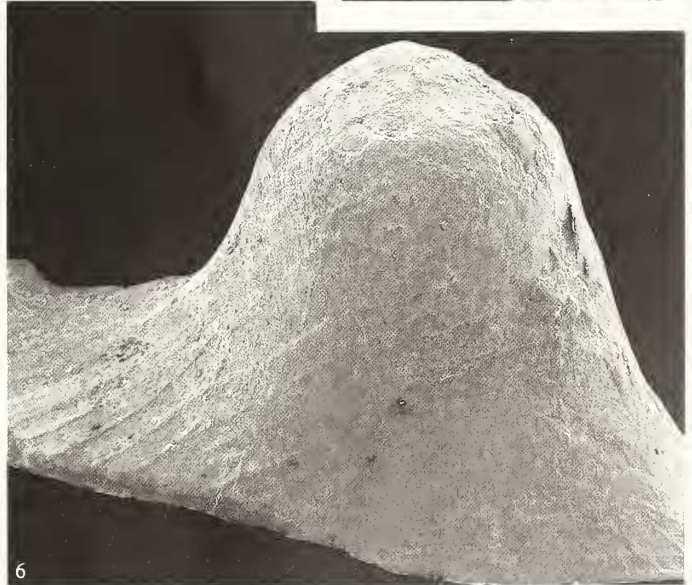
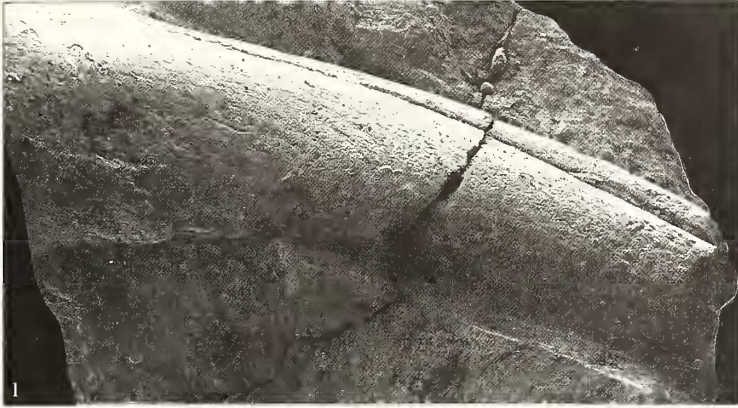
EXPLANATION OF PLATE 76

Figs. 1, 2. *Aspidoceras longispinum* (Sowerby). U.AC₂₁.5a.44, isolated lateral tubercle showing growth lines and longitudinal seam (adoral-umbilical view). Middle-Upper Kimmeridgian, 1, × 14, 2, × 26.

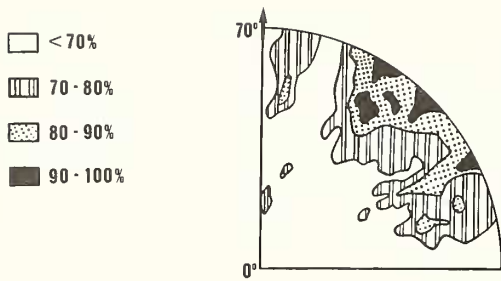
Figs. 3, 4. *Aspidoceras hystricosum* (Quenstedt). U.AC₂₁.5a.126, isolated lateral tubercle showing subcircular distal aperture (umbilical oblique view), Middle-Upper Kimmeridgian, 3, × 15, 4, × 32.

Figs. 5, 6. *Orthaspidoceras zieglerei* Checa. 5, U.AC₂₁.5a.36, isolated umbilical tubercle showing growth lines (umbilical view), Lower-Middle Kimmeridgian, × 13. 6, U.AC₂₁.5b.26, isolated umbilical tubercle showing growth lines (apical-ventral view), Lower-Middle Kimmeridgian, × 16.

SEM photographs. All specimens from Alta Coloma (province of Granada).



CHECA and MARTIN-RAMOS, *Aspidoceras*, *Orthaspidoceras*



TEXT-FIG. 3. Stereographic projection between 0° and 70° in the upper hemisphere of incomplete reflection $\{110\}$ pole figures of the calcite of an umbilical tubercle of *Aspidoceras sesquinodosum* Fontannes (U.AM₁-1.4). Note that the $\{110\}$ poles are perpendicular to the c axis. The axis of the spine is marked by the arrow. Only the 70%, 80% and 90% equilevel lines are shown.

different from that described for the shell-wall of ammonites (see e.g. Kulicki 1979; Birkelund 1981), where the c axes of the aragonite or vaterite crystals are perpendicular to the wall. This idiosyncratic alignment of the crystals is most probably the result of the mode of growth of the tubercles of *Aspidoceras* (see below).

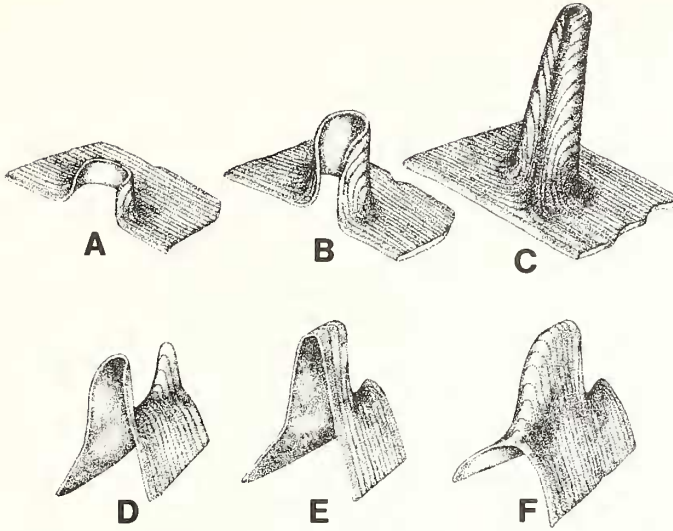
Growth pattern

We have reconstructed the way the spines grew by SEM observation of the growth lines of some of the best-preserved specimens (Pl. 76, figs. 1 and 2). On the adoral side the lines initially rise very close together and more or less perpendicularly to the spiral before spreading out and arching progressively backwards until they circumscribe apically the entire tubercle. This distribution suggests that the tubercle started life as an incomplete circle or horseshoe at the edge of the aperture (text-fig. 4A) and that the subsequent addition of incomplete, distorted rings of shell (text-fig. 4B) gradually formed a hollow, slightly conical spine (text fig. 4C). A characteristic feature of the tubercle is the seam running up the entire adoral side where the returning growth lines fuse with the outgoing ones (Pl. 76, figs. 1 and 2), indicating that the tubercle would have been all but fully grown by the time the mantle continued onward in its development. This growth pattern is similar to that reported for the spines in the bivalves *Crassostrea* (Rudwick 1965), *Etheria* (Carter 1968) and the gastropod *Murex* (Paul 1981).

As a comparison we have also examined the tubercular growth of another aspidoceratid, *Orthaspidoceras*. This genus has only one, periumbilical row of short, massive, mammiform tubercles, which were without a shadow of a doubt closed at the end. Furthermore, the growth lines of these tubercles indicate a completely different pattern of development, rising from the mantle parallel to each other and to the aperture (Pl. 76, figs. 5 and 6). This implies a fairly simple growth sequence in which the tubercle was formed at the same time as the mantle moved forward by the consecutive addition of protuberant waves of shell at its aperture (text-fig. 4D-F).

This would appear to mean that there was no single mode by which ammonite tubercles were formed, rather that it depended on their final morphology, which in turn was related, at least partly, to their function. The growth pattern seen in *Aspidoceras* would have been an unnecessarily complex way of producing short, mammiform tubercles, while on the other hand the orthaspidoceratoid pattern would have been entirely unsuitable for the growth of long, open-ended spines, which, if only half-formed along their entire longitudinal axis, would have become impossibly fragile during their development.

Some phylogenetic observations may also be made with regard to these two different modes of tubercle construction. *Aspidoceras* probably has its origin in the Oxfordian genus *Euaspidoceras*, which also has a seam along its tubercles (see Arkell 1940, pl. 41, fig. 4c), and which in turn is probably a descendant of *Mirosphinctes* gr. *nirus* in the lower Oxfordian. This latter genus is notable for its well-developed, parabolic, lateroventral nodes; in fact the tubercles of *Aspidoceras* in their initial growth stages bear a resemblance to parabolic nodes (text-fig. 4A). The forebears of *Orthaspidoceras* are not immediately obvious but it probably originated, by way of *Physodoceras*, from the Upper Oxfordian genus *Clambites*, which was partly descended from the Lower Oxfordian *Peltoceratoides*, whose tubercles were merely lumps on the lateroventral side of the ribs. That is to



TEXT-FIG. 4. Successive stages in the formation of tubercles in *Aspidoceras* (A–C) and *Orthaspidoceras* (D–F). See text for further explanation.

say that parabolic nodes appear nowhere in the phylogenetic succession stretching from *Peltoceratoides* to *Orthaspidoceras*. The above phylogenetic conclusions derive from research currently being carried out by A. Checa.

All this suggests that there is a clear phylogenetic component involved in the construction process of the tubercles. This partly inherited faculty would constitute a historical–phylogenetic factor according to Seilacher's (1970) use of the term.

FUNCTIONAL INTERPRETATION

Functional possibilities

Among the many hypotheses commonly put forward to explain the purpose of ammonite tubercles, perhaps the most widespread is that of defence against predators (see Westermann 1971, Kennedy and Cobban 1976). As far as *Aspidoceras* is concerned, the idea that its tubercles might have presented an active deterrent against a predator breaking the shell seems hardly likely (despite their sharp, pointed tips) as the wall of the immature spines, at least, is too fragile to have played such a defensive role. Furthermore, they curve forward slightly, to the extent that loads exerted at the tip would develop hinge points somewhere along the length of the spine, which would then easily give way and break (text-fig. 2B, D). This does not of course rule out the possibility that they may have provided some degree of dissuatory defence, giving the shell a somewhat alarming aspect. Anyway, it seems undeniable that the surface enveloping both rows of spines would have increased the ammonite's total volume, making it more difficult for large predators to catch and swallow it whole, as suggested by Paul (1981, p. 290) for *Murex*.

According to Kennedy and Cobban (1976, p. 30), the blocked-off tubercles may have been full of water and acted as horizontal stabilizers to prevent yawing when swimming and diving. In the case of *Aspidoceras* the floored tubercles could well have admitted sea water but their contribution to the shell's stability is not immediately apparent. Westermann (1971, p. 7) made an interesting comment with regard to this last point when he wrote that the basal septum would have protected the phragmocone against inflow of water in case of tubercle breakage. This protective role of the

basal septum in *Aspidoceras* is undeniable as it forms the only barrier between the interior of the phragmocone and the sea water.

It is worth mentioning that hollow spines could have gathered water, from which food would have been filtered afterwards, as in the bivalve *Crassostrea echinata* (Paul 1975, p. 20). This would lead us to attribute to *Aspidoceras* a marked micropagy. Although such an alimentary specialization cannot be excluded (Lehmann 1988), it would be unique among ammonites (and recent cephalopods, according to Nixon 1988), as their parrot-beak-shaped jaws (*Rhyncholites*) and radulae, which seem to be general in Jurassic ammonites (Lehmann 1981), could not have fulfilled that function.

Sensory function

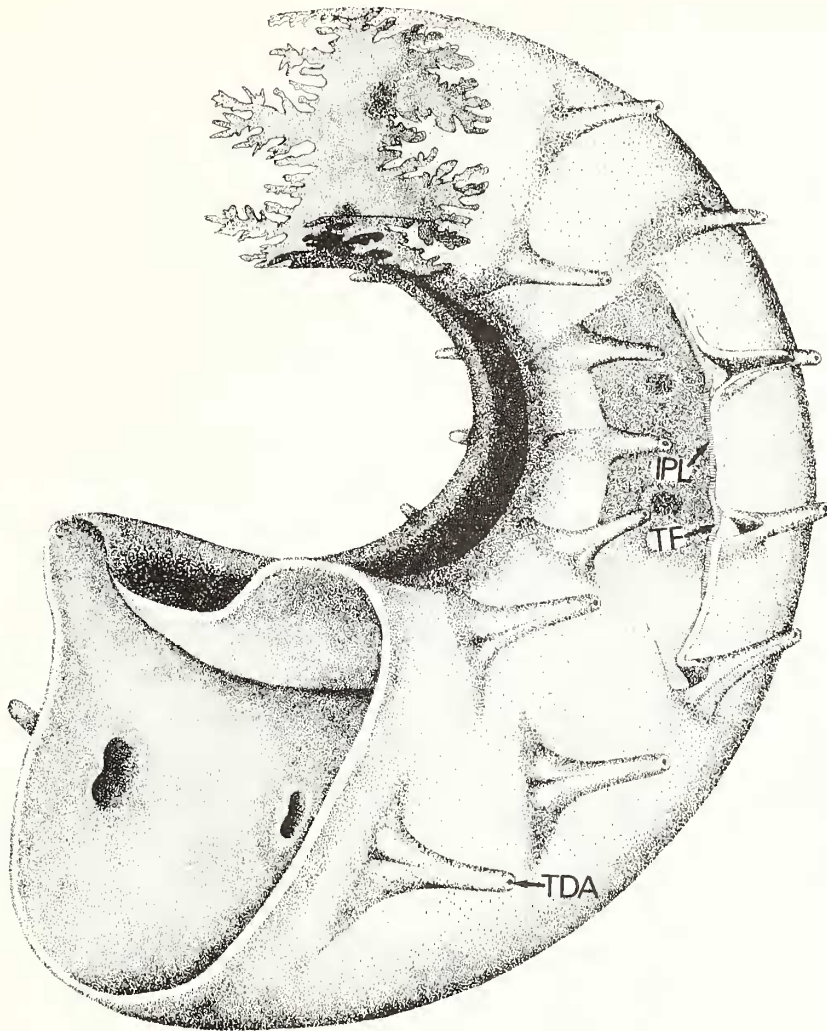
Without doubt the most important feature of the tubercles of *Aspidoceras* is that they were hollow and that their distal points were open. As has been mentioned before, at the foremost part of the body-chamber these spines were not sealed off at the base and the mantle-tissue must have been in contact with the environment (text-fig. 5). This must have been the case for the last-formed spines throughout the entire ontogeny.

The most probable role of these extensions of the mantle would have been to enhance the animal's sensory contact with its immediate environment, much in the same way as that described by Rudwick (1965) for the tubular spines of the brachiopods *Acanthothiris*, *Acanthorhynchia* and the bivalve *Crassostrea*, where, based on observations of the mantle properties of living brachiopods, he suggested that their function would have been essentially tactile and/or photo-chemo-sensitive.

The tubercles of *Aspidoceras* may, on the other hand, have had a somewhat different function. Brownell and Farley (1979) have reported the interesting manner in which the desert scorpion *Paruroctonus mesaensis* detects its prey by integrating the responses received from several mechano-sensory organs. This scorpion has mechano-receptors in the tarsal segments of its eight legs, which are capable of detecting the vibrations of its prospective prey moving across the sand. One of Brownell and Farley's most significant conclusions is that *P. mesaensis* can apparently perceive, within a certain radius, both the direction and distance of its prey, and that it achieves this by differentiating between the times of arrival of the stimulus at its various sensory organs. The eight legs of the scorpion when extended form an approximately circular sensory field of 4 to 6 cm in diameter in which the sensory receptors are regularly spaced on the ground plane. This disposition allows it to discern differences in arrival times of as little as 0.2 milliseconds.

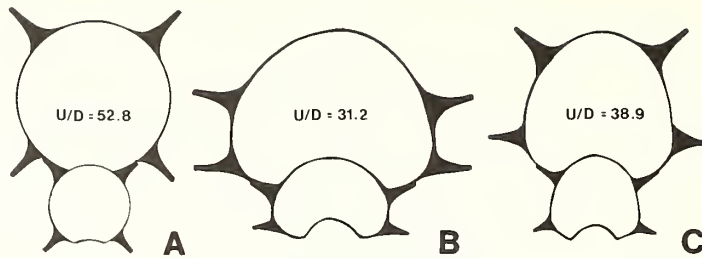
In like manner the two rows of floorless spines on either side of the forward part of the body chamber of *Aspidoceras* may well have formed two symmetrical sensory fields. The spines of each field would have been disposed along a more or less trapezoidal sector of the ammonite spiral (text-figs. 1A and 5). There are usually between three and six external floorless spines and between two and four internal ones. The number of tubercles in the lateral row is slightly more than that in the periumbilical one. This can be satisfactorily explained if it is borne in mind that the length of the spiral along the outer flank is greater than along the inner one and that the extra number of spines would offset this discrepancy, maintaining a regular distance between the tubercles of each row. This regularity in sensory receptors in *Aspidoceras* suggests some similarity in distribution to those of *Paruroctonus*.

Nevertheless, there are differences worth commenting on between the distribution of spines in *Aspidoceras* and the ideal distribution in a sensory system. Sensor distribution in *Paruroctonus*, regularly spaced on the ground plane, seems to be close to the paradigm for a predator hunting on a substrate. Given that *Aspidoceras* could have detected stimuli coming from any direction in an aqueous (three-dimensional) environment, the ideal distribution would have meant a uniform spacing between the sensors along the whorl cross-section, with the spines perpendicular to the shell (text-fig. 6A). However, in *Aspidoceras* sensors must have been disposed on two planes more or less parallel to the equatorial one on both sides of the organism (text-fig. 5); as a result, the spines are closer together on the flanks than on the venter (text-fig. 6B, C). Perhaps there could have been some fabrication noise involved in the distribution of the spines in *Aspidoceras*, as the outer row sets



TEXT-FIG. 5. Reconstruction of the living-chamber of *Aspidoceras* (in approximate life position) with a sector of the flank removed to show internal features. IPL, inner prismatic layer; TF, tubercle floor; TDA, distal aperture of the tubercle.

the limit of maximal overlapping between consecutive spirals and the ideal distribution would have required outer tubercles which were more external and, hence, a less overlapping (more evolute) spiral than is usually found in *Aspidoceras*. In fact, the evolution of *Aspidoceras* is marked by a progressive uncoiling and the subsequent separation of the two rows of tubercles (Checa 1985, p. 297), with a tendency throughout the phylogeny for the external row of tubercles to move towards the outermost part of the shell's flank. If it were true that the tubercles did in fact play a mechano-sensory role, then this displacement would have resulted in a keener sensory threshold and thus it may be concluded that the genus *Aspidoceras* evolved in the direction of greater mechano-sensory specialization. In this sense it is worth mentioning that the most evolute species of *Aspidoceras* (the Upper Kimmeridgian *A. apenninicum* Zittel) is closer to the paradigm than the remaining, more involute species of *Aspidoceras* (text-fig. 6C).



TEXT-FIG. 6. Variation in the distribution of spines along the whorl cross-section with the uncoiling in *Aspidoceras*, and comparison with the ideal distribution of the sensors (paradigm). A, paradigm. B, *Aspidoceras binodum* (Oppel), U.C₂. 10. 10, Sierra de Cabra (province of Córdoba), Lower Kimmeridgian. C, *Aspidoceras apenninicum* Zittel, U.AC₂₁. 5a. 103, Alta Coloma (province of Granada), Middle–Upper Kimmeridgian. U/D, Umbilicus/Diameter ratio.

One additional point of interest is that the only stimulus detectable to the aspidoceroid mechanoreceptors would have been longitudinal compression waves (P waves) as the transverse waves (S waves) are not transmitted in water and the surface waves (Rayleigh and Love waves) would only be detected by an organism resting on top of the substrate (such as *Paruroctonus*). The speed of the P waves is proportional to the square root of the rigidity of the medium through which they are being transmitted, so they travel comparatively more slowly in liquids than in solids. If the information obtained by the animal is based on a difference in time between the stimulation of various receptor organs then a slower transmission speed will increase the capacity to determine both the source and the distance of the stimulus. This being true *Aspidoceras* would have been much more sensitive to its environment than *Paruroctonus*, even when very young and with relatively little distance between its ‘antennae’.

During the ontogeny of *Aspidoceras*, as new spines were being created at the aperture of the shell, so older ones were abandoned by the sensitive tissue of the mantle and closed off by a layer of inner prismatic shell. Each tubercle must have been filled, from the moment of its genesis to its being blocked off, by a continuous progression of mantle tissue, which was constantly moving towards the growing edge of the shell, so that the relative positions between any tubercle and the nerve endings occupying its tip would have been constantly changing. This interpretation implies the existence of a continuous lateral band of sensitive material coinciding with each row of tubercles, two on each flank in the case of *Aspidoceras*. This arrangement is remotely reminiscent of the lateral sensory lines that many living fishes have.

Alternatively, we may suppose an analogous mechanism to that described by Paul (1981, p. 289) for the gastropod *Murex pecten*. At a given moment during growth, mantle epithelium proliferated into long extensions (one for each non-floored spine) which developed special sensory tissue at their distal tips. These extensions remained fixed until the forward movement of the mantle restarted, when they would be resorbed again. This process only makes sense if growth at the aperture in *Aspidoceras* was intermittent (episodic), as in *Murex*. Nevertheless, the uniform distribution of growth lines observed in some well-preserved specimens of *Aspidoceras* makes this alternative highly problematic.

In view of the abundance of tuberculate forms throughout the Mesozoic it may be advisable to review the role played by the tubercles in other ammonites to ascertain whether they may not have had some sensory function.

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